6-21-2010

Resolving Issues of Imprecise and Habitat-Biased Locations in Ecological Analyses Using GPS Telemetry Data

Jacqueline L. Frair
SUNY College of Environmental Science and Forestry, jfrair@esf.edu

John Fieberg
Minnesota Department of Natural Resources

Mark Hebblewhite
University of Montana - Missoula, mark.hebblewhite@umontana.edu

Francesca Cagnacci
Research and Innovation Centre, Environment and Natural Resources Area, Edmund Mach Foundation

Nicholas J. DeCesare
University of Montana - Missoula

See next page for additional authors

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2010) **365**, 2187–2200
doi:10.1098/rstb.2010.0084

Review

Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data

Jacqueline L. Frair[1,*], John Fieberg[2], Mark Hebblewhite[3], Francesca Cagnacci[4], Nicholas J. DeCesare[3] and Luca Pedrotti[5]

[1]*SUNY College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA*
[2]*Biometrics Unit, Minnesota Department of Natural Resources, 5463-C W, Broadway Forest Lake, MN 55025, USA*
[3]*Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA*
[4]*Research and Innovation Centre, Environment and Natural Resources Area, Edmund Mach Foundation, 38010 San Michele all'Adige, Trento, Italy*
[5]*Stelvio National Park, 23032 Bormio, Sondrio, Italy*

Global positioning system (GPS) technologies collect unprecedented volumes of animal location data, providing ever greater insight into animal behaviour. Despite a certain degree of inherent imprecision and bias in GPS locations, little synthesis regarding the predominant causes of these errors, their implications for ecological analysis or solutions exists. Terrestrial deployments report 37 per cent or less non-random data loss and location precision 30 m or less on average, with canopy closure having the predominant effect, and animal behaviour interacting with local habitat conditions to affect errors in unpredictable ways. Home-range estimates appear generally robust to contemporary levels of location imprecision and bias, whereas movement paths and inferences of habitat selection may readily become misleading. There is a critical need for greater understanding of the additive or compounding effects of location imprecision, fix-rate bias, and, in the case of resource selection, map error on ecological insights. Technological advances will help, but at present analysts have a suite of ad hoc statistical corrections and modelling approaches available—tools that vary greatly in analytical complexity and utility. The success of these solutions depends critically on understanding the error-inducing mechanisms, and the biggest gap in our current understanding involves species-specific behavioural effects on GPS performance.

Keywords: home range; missing data; movement models; radiotelemetry; resource selection; measurement error

1. INTRODUCTION

Radio-collars and other platforms equipped with global positioning systems (GPS) document animal activity under cloak of darkness and inclement weather conditions, providing a continuous record of animal locations that remains unobtainable using traditional technologies such as very high-frequency (VHF) devices (White & Garrott 1990; Beyer & Haufler 1994; Rogers *et al.* 1996; Tomkiewicz *et al.* 2010). The systematic and frequent recording of animal locations by on-board GPS units facilitates greater resolution in the study of habitat selection (Johnson *et al.* 2002*b*; Boyce *et al.* 2003), deeper insight into animal movements (Morales *et al.* 2004; Frair *et al.* 2005; Fryxell *et al.* 2008), and novel investigations into animal behaviour (e.g. Anderson & Lindzey 2003; Merrill *et al.* 2010). Although GPS applications have transformed contemporary wildlife studies (Hebblewhite & Haydon 2010), the technology comes with its problems. High up-front unit costs, rare but catastrophic equipment failures (i.e. computer glitches or failed breakaway devices), and trade-offs between GPS location collection intervals and unit longevity lead generally to fewer monitored individuals and shorter study durations compared with VHF-based studies (Johnson *et al.* 2002*a*; Gau *et al.* 2004; Hebblewhite *et al.* 2007). Moreover, decreasing the interval between recorded locations increases the level of autocorrelation in the resulting data. As a result, analysts of GPS telemetry data face even greater challenges for deriving population-level inferences (Lindberg & Walker 2007; Fieberg *et al.* 2010).

Fundamentally, instruments imply measurement errors (Cagnacci *et al.* 2010). Problems inherent to both VHF and GPS devices are spatial imprecision

* Author for correspondence (jfrair@esf.edu).

One contribution of 15 to a Theme Issue 'Challenges and opportunities of using GPS-based location data in animal ecology'.

and potential biases in the locations acquired. The accuracy of GPS locations do not typically include a directional bias (Moen *et al.* 1996; Sager-Fradkin *et al.* 2007), but are subject to variability in precision measured as the distribution of differences between the true (central) location and GPS-estimated locations. Therefore, we use 'precision' or 'measurement error' rather than 'accuracy' when addressing the distribution of spatial error in GPS locations. Precision on the order of 200–600 m has been reported for locations of VHF devices acquired via triangulation and homing (White & Garrott 1986; Marzluff *et al.* 1994; Zimmerman & Powell 1995). In contrast, measurement errors of 100 m or less were reported for early model GPS collars between their first deployment in the mid-1990s and the removal of selective availability in 2000 (Rempel *et al.* 1995; Rogers *et al.* 1996), after which time a precision of 10–28 m has consistently been observed (D'Eon *et al.* 2002; Cain *et al.* 2005; Hansen & Riggs 2008). Nevertheless, large measurement errors (up to several km) intermittently occur even with contemporary GPS devices (e.g. Villepique *et al.* 2008), which complicate analyses using these data. Moreover, with GPS devices, biases occur when locations are more likely to be obtained under certain environmental conditions. Failed locations are not unique to GPS devices, with inclement weather, darkness and poor access to areas reducing our ability to detect VHF devices (White & Garrott 1990; Keating *et al.* 1991; Moen *et al.* 1996; North & Reynolds 1996). Such conditions are generally study specific and difficult to quantify in VHF-based studies. In contrast, local habitat conditions predictably influence the ability of GPS devices to acquire satellite signals, thus systematically biasing the set of locations acquired but also making it possible to quantify the biasing mechanism so as to employ statistical corrections (D'Eon 2003; Frair *et al.* 2004). For clarity, we reserve the term 'bias' for the bias in acquiring a GPS location rather than as a component of spatial error in the locations acquired. We refer to bias and measurement error collectively as 'GPS errors'.

GPS technology poses unique opportunities for wildlife studies, but proper statistical inference requires attention be paid to the inherently autocorrelated, spatially imprecise and habitat-biased locations acquired by current systems (but see the emerging technologies in Tomkiewicz *et al.* 2010). Fieberg *et al.* (2010) focus exclusively on the implications of correlated data and review contemporary solutions. Herein, we review the magnitude and source of contemporary GPS errors; consider the implications of these errors in studies of animal resource selection, movements and home range; and summarize the toolbox of solutions available to data analysts. Lastly, we chart ongoing needs for research on GPS errors in animal ecology. Note that we limit this review to studies employing devices reliant on the NAVSTAR GPS satellite system and deployed mainly on terrestrial species (Rodgers *et al.* 1996), because the range of systems (e.g. Loran, Argos) and their inherent errors are too great to succinctly summarize here. Nevertheless, the analytical issues and solutions discussed are generally adaptable to these other systems as well.

2. TYPES, MAGNITUDE AND CAUSES OF GPS ERRORS

Problems associated with animal-borne GPS devices have been elucidated using three primary methods: stationary tests, controlled mobile tests and returns from free-ranging animals. With stationary tests, devices are typically affixed 0.5–1.5 m above ground to simulate the neck height of standing animals, or placed on the ground (with collar designs placed upright or on their sides) to simulate bedded animals. These devices attempt to acquire locations (or 'fixes') at a pre-determined temporal interval (usually every 5 min to 2 h) and are left in place for a given period of time (usually 24 h or more). The number of successful fixes (stored locations) divided by the number attempted yields the fix rate, and the precision of locations is quantified as the average distance between each estimated location and the 'true' location of the device (the latter determined using fixed geodetic markers, differential-correction or a large-sample average). For optimal performance, tests should deploy GPS devices on a medium that mimics the ground-plane of an animals' body (e.g. balloon filled with saline solution). Stationary tests are particularly useful because they remove vagaries arising when devices are deployed on animals, can be replicated across a range of spatial and temporal variation, and are readily comparable among study sites and time periods. By contrast, mobile device tests affix a GPS device to a human, vehicle or tame animal generally moving at a speed of approximately 3–10 kph, with 'true' locations estimated by following the moving device with a handheld unit. Such studies provide unique insights into motion effects on GPS performance, but are less comparable across species, study sites and time periods, and represent a limited range of behaviour and ecological conditions compared with free-ranging animals. Finally, returns from free-ranging animals yield fix rates and some information on location precision (e.g. proportion of locations in the more precise 'three-dimensional' mode), but the conditions causing GPS errors cannot be directly assessed unless animals are also physically observed by researchers (see Heard *et al.* 2008). Free-ranging animal returns are least comparable among species, study areas and time periods, but nonetheless provide information critical to understanding animal behaviour and refining controlled tests.

We know from stationary tests that canopy closure (Moen *et al.* 1996; D'Eon *et al.* 2002; Frair *et al.* 2004; Cargnelutti *et al.* 2007; Hebblewhite *et al.* 2007; Sager-Fradkin *et al.* 2007; Heard *et al.* 2008), topographic complexity (D'Eon *et al.* 2002; Frair *et al.* 2004; Cain *et al.* 2005; Hebblewhite *et al.* 2007), device orientation (Moen *et al.* 1996; D'Eon & Delparte 2005; Sager-Fradkin *et al.* 2007; Heard *et al.* 2008; Jiang *et al.* 2008), scheduled fix interval (Cain *et al.* 2005) and device make/model (Frair *et al.* 2004; Hebblewhite *et al.* 2007) consistently influence both fix rate and location precision (table 1). Less consistently, researchers have observed diurnal (Sager-Fradkin *et al.* 2007, but see Graves & Waller 2006), seasonal (Sager-Fradkin *et al.* 2007) and tree height or density effects (Rempel *et al.* 1995; Rumble & Lindzey

Table 1. Summary of GPS fix rates and measurement errors reported by stationary tests of wildlife monitoring devices in terrestrial environments. Reported values are the range of mean values reported across the studies indicated.

	effects on	
variable	fix rate reduction (%)	measurement error (m)
canopy closure[a,b]		
0–40%	1–10[c,d,e,f,g,h,i,j,k]	7–13[c,e,h]
41–70%	1–25[c,d,e,f,g,h,i,k]	16[c,e]
>70%	2–37[c,d,e,f,g,h,i,j,k]	19–30[c,e,h]
topography (available sky)[l,m]		
>60% AS	0–1[c,n]	0–5[c,n]
30–60% AS	1–2[c,n]	5–7[c,n]
<30% AS	4–8[c,n]	10–13[c,n]
collar orientation		
0–45°	0–6[o,g]	3–6[o]
90° (above ground)	1–16[o,i]	10[o]
90° (on ground)[l]	16–80[d,g]	
135–180°	12–24[o]	17[o,p]
fix interval		
0.5 h	1[n]	no effect[n]
1 h	3[n]	
4 h	6[n]	
6+ h	8[n]	
collar brand, model[q]		
Lotek 1000	10–30[i,r,s]	60[s]
Lotek 2200L	4–14[e,j]	13[e]
Lotek 3300	1–7[e,h,j,k,p]	14–28[e,h,k,p]
Televilt Simplex	6–24[j,d,g]	
ATS	3–5[c,j]	11[c,o]
Telonics (3580)	4[n]	10[n]

[a]Effects observed to vary with collar brand and model (Frair *et al.* 2004; Hansen & Riggs 2008).
[b]Effects observed to vary with terrain complexity (Sager-Fradkin *et al.* 2007).
[c]D'Eon *et al.* (2002).
[d]Sager-Fradkin *et al.* (2007).
[e]Hansen & Riggs (2008).
[f]Frair *et al.* (2004).
[g]Heard *et al.* (2008).
[h]Cargnelutti *et al.* (2007).
[i]Moen *et al.* (1996).
[j]Hebblewhite *et al.* (2007).
[k]Lewis *et al.* (2007).
[l]Effects observed to vary with canopy closure (Jiang *et al.* 2008; Sager-Fradkin *et al.* 2007; Heard *et al.* 2008).
[m]Other terrain variables influencing collar errors include topographic position (Hebblewhite *et al.* 2007), aspect (Hebblewhite *et al.* 2007) and per cent slope (Frair *et al.* 2004; Hebblewhite *et al.* 2007).
[n]Cain *et al.* (2005).
[o]D'Eon & Delparte (2005).
[p]Jiang *et al.* (2008).
[q]Averaged across canopy cover and terrain conditions.
[r]Dussault *et al.* (1999).
[s]Rempel *et al.* (1995).

1997; Dussault *et al.* 1999). The effects of canopy closure on GPS errors remain predominant, reducing fix rates up to 37 per cent and location precision by 12–17 m on average (table 1). Canopy closure may interact with local terrain complexity resulting in even greater errors (D'Eon *et al.* 2002; Frair *et al.* 2004; Hebblewhite *et al.* 2007; Hansen & Riggs 2008). Excluding canopy effects, terrain complexity alone may result in an 8 per cent or less reduction in fix rates and 10–13 m measurement error on average (D'Eon *et al.* 2002; Cain *et al.* 2005). Collar orientation alone tends to have a negligible effect on GPS errors in open areas, but can reduce fix rates up to 80 per cent and location precision as much as 17 m under dense canopy cover (Heard *et al.* 2008; Jiang *et al.* 2008). Cain *et al.* (2005) observed that reducing the frequency with which locations were collected, from every 15–30 min to every 6–13 h, reduced fix rates up to 8 per cent without affecting location precision. Finally, GPS hardware and software varies among manufacturers and manufacturing cycles, with earlier models, e.g. Lotek GPS1000, exhibiting 10–30% data loss and 60 m measurement error on average across various canopy and terrain conditions (Rempel *et al.* 1995; Moen *et al.* 1996; Dussault *et al.* 2001). Contemporary models (Lotek 2200 and 3300, Televilt Simplex, ATS, Telonics) exhibit data losses from 1 to 24 per cent and measurement errors less than 28 m on average (table 1).

Stationary tests have also been used to explore the effects of satellite number and configuration on location precision. With each acquired location, GPS devices store additional information on the number of satellites used in the location solution, and an index to satellite geometry based on a dilution of precision (DOP) metric. Lower DOP values indicate wider satellite spacing, and tests reveal a general, albeit noisy, trend of decreasing spatial precision with increasing DOP values (Moen *et al.* 1996; Lewis *et al.* 2007) Along with DOP, GPS devices record whether the solution is in two-dimensional (based on three satellites) versus three-dimensional mode (based on four or more satellites, which includes a correction based on device elevation). On average, two-dimensional locations exhibit less precision ($\bar{x} \leq$ 36 m) than three-dimensional locations ($\bar{x} \leq 12$ m; Moen *et al.* 1996; D'Eon *et al.* 2002; Graves & Waller 2006; Lewis *et al.* 2007; Sager-Fradkin *et al.* 2007; Jiang *et al.* 2008), and researchers recommend separate consideration of these two classes of data when choosing to censor locations, as we shall consider in depth later. In addition to biasing whether a location is collected or not, canopy closure and terrain ruggedness explained 52–71% of the variation in mean measurement error, proportion of locations collected in a three-dimensional mode, and mean DOP values in stationary device tests (Lewis *et al.* 2007), with canopy closure having the greatest explanatory power.

Controlled mobile tests are rare, and their results less consistent than stationary tests, nonetheless their insights into the effects of animal behaviour and mobility on GPS performance are compelling. Bowman *et al.* (2000) observed that fix rates were reduced by up to 20 per cent when captive white-tailed deer (*Odocoileus virginianus*) were bedded compared to when they were standing or moving. Observations of captive moose (*Alces alces*) and white-tailed deer indicated no significant differences in either fix rate or location precision when animals were moving compared to when the animals remained stationary (Moen *et al.* 1996; Bowman *et al.* 2000); however, both of these studies were conducted using older

model GPS devices that had lower baseline precision and fix rates compared with contemporary models (but see back-pack trial of Edenius 1997). More recently, Cargnelutti *et al.* (2007) fitted an English setter with a GPS collar and observed lower fix rates but no differences in location precision when the animal was moving compared with stationary tests. An interaction between movement and forest cover was observed by Jiang *et al.* (2008) using devices affixed to a vehicle moving approximately 10 kph. Jiang *et al.* (2008) documented reductions in both fix rates and the proportion of fixes in a three-dimensional mode when moving through forest but not through open areas.

Importantly, fix rates recovered from free-ranging mammals wearing GPS collars averaged 5–33% lower than stationary collar tests (Biggs *et al.* 2001; Cain *et al.* 2005; Hebblewhite & Merrill 2007; Lewis *et al.* 2007; Sager-Fradkin *et al.* 2007). From terrestrial studies of various large mammal species and collar brands since 2001, researchers have observed fix rates in the range of 43–99% (Gau *et al.* 2004; Graves & Waller 2006; Hebblewhite *et al.* 2007; Lewis *et al.* 2007; Sager-Fradkin *et al.* 2007; Brooks *et al.* 2008; Heard *et al.* 2008) that tend to vary both diurnally (Biggs *et al.* 2001; Graves & Waller 2006; Sager-Fradkin *et al.* 2007; Heard *et al.* 2008) and seasonally (Dussault *et al.* 1999; Sager-Fradkin *et al.* 2007, but see D'Eon & Serrouya 2005). Some temporal variation may be accounted for by satellite configuration and leaf-drop, but these effects have generally been trivial in stationary collar tests (e.g. Frair *et al.* 2004). The strong diurnal and seasonal forcing in fix rates observed for free-ranging animals is probably driven by animal behaviour and habitat choices. For example, Graves & Waller (2006) determined that fix rates for grizzly bears (*Ursus arctos*) were positively correlated with movement rate, which conflicts with the mobile device tests reported previously, and was not explained by variation in local satellite availability. Graves & Waller (2006) presumed this to be a function of collar orientation (largely vertical when bears were moving, and horizontal when resting) rather than an effect of movement *per se*. Using aerial telemetry, Heard *et al.* (2008) observed that bears tended to rest under forest cover and actively forage in open areas. Stationary tests revealed an interaction between collar position (on the ground to simulate bedding) and canopy cover that, when combined with the diurnal activity patterns of bears, explained the low fix rates observed for free-ranging bears (Heard *et al.* 2008). These studies demonstrate how combining visual observations of animal activity with stationary tests forges strong linkages among animal behaviour and GPS performance. Where possible more such studies are needed to understand the generality of animal behaviour effects on GPS errors.

Negative correlations between fix rates and grizzly bear body size (neck circumference, girth and weight) have also been observed (Graves & Waller 2006). This may have resulted from improperly fitted collars, which are not one size fits all but tailored specifically to a small range of neck circumferences. Moreover, in their study female bears were smaller than male bears, and sex-specific behavioural differences also could have played a role in GPS functioning. We caution that differences according to body size within a species may not translate to differences among species because discrepancies in habitat selection would probably confound interpretation of body size effects on GPS performance (see also Hebblewhite *et al.* 2007).

3. IMPLICATIONS OF GPS ERRORS AND THE TOOLBOX OF SOLUTIONS FOR ECOLOGICAL ANALYSES

(a) *Resource selection*

Statistical detection of whether animals select or avoid certain conditions (White & Garrott 1986; Nams 1989; Rettie & McLoughlin 1999; Frair *et al.* 2004; Visscher 2006; Johnson & Gillingham 2008), the apparent magnitude of selection or avoidance (Frair *et al.* 2004; Visscher 2006; Johnson & Gillingham 2008) and the predictive ability of statistical models (Johnson & Gillingham 2008) are sensitive to both spatial imprecision and habitat biases in GPS location data. The magnitude of observed effects depends on the magnitude of imprecision and bias, GPS sampling interval, landscape grain (i.e. minimum mapping unit), habitat patchiness and the ecology of the species under study. Generally speaking, rare habitat types are subject to false negatives (type-II errors), whereas common types are subject to false positives (type-I errors). However, McKenzie *et al.* (2009) observed high type-I error rates for the use of linear habitat features, such as trails, which may not be rare *per se* but represent patches of small spatial extent with high amounts of edge. Changes in coefficients of selection generally become statistically important given biased data losses in the range of 10–25% (D'Eon 2003; Frair *et al.* 2004; Johnson & Gillingham 2008; Nielson *et al.* 2009). The effects of location imprecision, namely misclassifying the habitat type within which locations occur, are exacerbated by the size and interspersion of vegetation types (or habitat patches), and animal preference for edges (White & Garrott 1986; Nams 1989; Rettie & McLoughlin 1999; Visscher 2006; Johnson & Gillingham 2008). Given patch sizes that are smaller than the average location error, selection coefficients tend towards zero (White & Garrott 1986; Rettie & McLoughlin 1999; Johnson & Gillingham 2008). The effects of location imprecision and fix-rate bias on selection coefficients also are exacerbated by strong selection for a habitat or cover type, which is a function of both animal preference and habitat rarity (Frair *et al.* 2004; Visscher 2006; Johnson & Gillingham 2008). We know of only one study comparing the direct effects of both location imprecision and fix-rate bias on selection coefficients (Johnson & Gillingham 2008). In this simulation study, coefficients deviated significantly from 'truth' given spatial imprecision of 200 m or more or fix-rate bias of 25 per cent or more, each evaluated while holding the other type of error constant (at zero). Interestingly, Johnson & Gillingham (2008) further tested the effect of classification accuracy in the original habitat map on selection coefficients, and noted statistically significant differences given

misclassification rates of 10 per cent or more. Overall classification accuracy rates for Landsat-derived habitat data typically range approximately 60–90% (Stehman *et al.* 2003; Wickham *et al.* 2004; Mayaux *et al.* 2006), profoundly constraining the ecological question pursued and, by extension, the level of spatial precision required in animal locations. Further study is needed to explore how general these patterns are as well as to quantify the additive or compounding effects of location imprecision, fix-rate bias and map accuracy on inferences of selection. Moreover, attention needs to be paid to the gross mismatch between the fine-scale, temporally dynamic animal locations and the coarse-scale, static habitat maps we relate those locations to (Urbano *et al.* 2010).

To our knowledge there has been no solution proposed for overcoming both fix-rate bias and location imprecision in a single analysis. Recommendations for dealing with imprecise locations in studies of resource selection have included smoothing habitat maps by lumping rare cover types to increase patch sizes relative to location imprecision (but at the expense of resolution of inference), calculating proximity to all habitat types rather than assigning each location to a single habitat type (Conner *et al.* 2003, but see Dussault *et al.* 2005; Conner *et al.* 2005), censoring locations that occur on the edge of patches (which could eliminate large numbers of locations and introduce bias for edge-dependent species; Zimmerman & Powell 1995) or removal based on a DOP cutoff (which also may result in large and habitat-biased data losses; Rempel & Rodgers 1997; Lewis *et al.* 2007), buffering locations to replace points with areas of potential use (Kufeld *et al.* 1987; Rettie & McLoughlin 1999), buffering small-extent (high-edge) landscape features as a function of both location precision and width of the feature (McKenzie *et al.* 2009), resampling from a fitted or assumed error distribution to quantify uncertainty in misclassification rates (Nams 1989; Samuel & Kenow 1992; Kenow *et al.* 2001; Visscher 2006) or producing selection estimates that are weighted by misclassification rates (Nams 1989; Findholt *et al.* 2002; table 2). Whether replacing points with areas or resampling within error polygons, buffers introduce noise by including habitats that may not influence animal behaviour, and thereby reduce one's ability to statistically detect selection (Rettie & McLoughlin 1999). Exponential, bivariate normal, or bivariate Laplace distributions better reflect known distributions of spatial imprecision in GPS locations (Visscher 2006; McKenzie *et al.* 2009), and their use should introduce less noise compared with a uniform error distribution when buffering either animal locations or landscape features.

Censoring locations to improve the overall precision of the dataset is commonly employed, and begins with careful screening of implausible locations (e.g. a single location far outside the normal animal range requiring extraordinary speed). Lewis *et al.* (2007) showed that censoring based on values of positional DOP (PDOP) removes some grossly imprecise locations, effectively reducing the circular error probable (CEP; the radius of a circle containing a given percentage of locations assuming a bivariate normal distribution), but without reducing the average location precision *per se*. Depending on the choice of PDOP cutoff and the magnitude of location imprecision, the proportion of data removed by screening could be as large as 80 per cent (D'Eon & Delparte 2005; Lewis *et al.* 2007). Lewis *et al.* (2007) recommend screening only two-dimensional locations, and by removing two-dimensional locations having PDOP more than 5 they reduced 95 per cent CEP values ($CEP_{0.95}$) from 106.8 to 79.2 m while removing only 5.5 per cent of the locations. The same rule applied to free-ranging black bears (*Ursus americanus*) resulted in an 8.6 per cent data reduction on average, for an overall data retention rate of 80–90%, which we note falls within the range at which statistical errors manifest in resource selection studies. Importantly, given that canopy closure and terrain influence location precision, the intentional removal of imprecise locations occurs at the expense of increasing habitat-biased data loss.

Recommended solutions for the problems of biased missing locations have included sample weighting (Johnson *et al.* 1998; D'Eon 2003; Frair *et al.* 2004) and iterative simulation (Frair *et al.* 2004; table 2), both of which require a spatially predictive model for the probability of a GPS device successfully acquiring a fix (P_{fix}). With sample weighting, each acquired location is adjusted by $1/P_{fix}$, such that hard-to-acquire locations exert greater influence on model results. Sample weighting does not physically alter sample sizes by duplicating records or putting locations back in *geographical* space (*sensu* Aarts *et al.* 2008), i.e. the physical x, y and z (or depth) coordinates of a given missing location. Rather, by inflating the influence of hard-to-acquire locations weighting corrects for missing locations in *environmental* space (*sensu* Aarts *et al.* 2008), i.e. as a function of the suite of biotic and abiotic variables influencing P_{fix}. As such, adjusting the weight of each successfully acquired location may not account for the diurnal and seasonal forcing apparent in free-ranging animal location data unless the P_{fix} model includes covariates to capture those effects (e.g. see Sager-Fradkin *et al.* 2007). In the alternative approach, iterative simulation, a new location is probabilistically added to the dataset (based on P_{fix}) within the geographical realm of the missing location to complete multiple realizations of 'true' animal paths, with each realization analysed independently, and the results of multiple realizations combined using multiple imputation techniques (Frair *et al.* 2004). Related developments include the use of Brownian bridge models to reconstruct paths between locations based on a random walk process (Horne *et al.* 2007*a*; table 2). Such simulation approaches are more technically involved than sample weighting, but also may prove more advantageous because they provide corrections in both environmental and geographical space, and thus implicitly account for potential interactions between animal behaviour and local habitat conditions. Both iterative simulation and sample weighting approaches have been shown to reduce type-II error rates and correct biases in coefficient values (Frair *et al.* 2004, but see D'Eon 2003; Sager-Fradkin *et al.* 2007).

Table 2. Summary of proposed solutions for imprecise and biased missing locations in ecological analyses using GPS telemetry data.

proposed solution	description	benefits	considerations
increase sample sizes[a,b]	reduce location interval, or increase duration or number of animals monitored to acquire more locations	reduces standard errors around estimates, increases statistical power[a]	habitat-dependent bias and spatial imprecision not removed[c]
smooth habitat maps	lump rare types to increase patch size relative to measurement error	reduces misclassification of habitats used	reduces resolution of inference. does not account for biased missing data
censor edge locations	remove locations occurring on the edge of habitat patches	reduces misclassification of habitats used	potentially eliminates large numbers of locations, and introduces bias, especially for edge-dependent species
increase location accuracy by			
differential correction	store ephemeris data with locations, post-process locations to reduce imprecision using base station data collected simultaneously with animal-borne device	reduces measurement error to within 5 m on average[d]	reduces battery storage capacity, post-processing labor intensive, base station must be within 400 km[d]; does not fully remove canopy-induced errors[e]
DOP-based screening	remove data above DOP threshold, consider different thresholds for two-dimensional and three-dimensional locations[d,f]	removes grossly imprecise locations, reducing 95% circular error probable values, but does not improve mean location precision *per se*[f]	habitat-dependent error not removed[c], bias potentially exacerbated[f]; reduces sample sizes, and interrupts continuous path record[g]; should be conducted prior to modelling P_{fix} for sample weighting or iterative simulation (see below)
smooth animal paths by			
censoring inaccurate locations	buffer displacement between pairs of locations separated by 1 time lag (buffer representing location imprecision), remove intervening location if within buffer[h]	straightens tortuous paths[h]	appropriate buffer difficult to specify, varies with habitat and behaviour; removing locations reduces sample samples sizes and disrupts continuous path trajectory[g]
fitting spline to trajectory	fit spline through point trajectory[h]	removes fine-scale jitter from path; interpolates information to areas between acquired fixes assuming straight-line travel between fixes	continuous line no longer corresponds to original path sampling intervals[h]; can introduce error into accurate locations; path must be re-segmented to estimate turn angle and step length
resampling fix intervals	specify fix interval based on animal movement propensity, GPS location precision, and average habitat patch size[i]	minimizes falsely concluding animal movement[g], and misclassification of patch use[i]	longer fix intervals will reduce sample size, potentially reduce fix rates[j], and may underestimate total daily movement
removing resting bouts	identify periods of animal inactivity using activity sensors, movement rates, or predictive models	step length and turn angle distributions more accurate, based on actual moves	resting confounded with fine-scale foraging behaviour, may underestimate total movement and time spent active
resample locations within error polygons	buffer locations by predicted level of imprecision, generate random sample of locations within buffer; can model location imprecision $\sim f$(collar, time, canopy cover, terrain conditions, and animal activity)	reduces misclassification rates; untested for reducing coefficient bias or errors in predictive success of models; may be readily combined with iterative simulation for missed fixes	distribution of error for re-sampling should be bivariate normal[k] or bivariate laplace[l] (uniform distribution introduces excessive noise[m])

(*Continued.*)

Table 2. (*Continued.*)

proposed solution	description	benefits	considerations
buffer habitat 'patch' by location imprecision	buffer linear or other small-extent (high edge) patches, e.g. roads, $\sim f$(GPS precision and width of habitat feature)[l]	reduces type-I errors with little sacrifice of type-II errors	error distribution of Lotek 3300_s followed bivariate laplace distribution under conifer cover[l]; need broader testing by habitat type and collar brand; does not correct for missing locations
replace points with areas	use location precision to define area used by animal, analyse composition of area rather than habitat at points[c,n] or simulate points to calculate misclassification rates[a,o,k,n]	corrects relative ranking of habitats used, and direction of effects[c]	buffers include noise and reduce ability to detect selection[c]; applicable only for categorical variables
apply sample weights			
to missing locations	adjust the influence of acquired locations so as to represent lost data. Model $P_{\text{fix}} \sim f$(collar, time, canopy cover, terrain conditions, animal activity), and use $1/P_{\text{fix}}$ as sample weight[p,s,t]	reduces type-II errors and corrects coefficient bias when estimating habitat selection given correctly specified bias model[p]. Can produce unbiased home range estimate[u]	developing bias model requires independent field surveys[p,q,r], and bias mechanism may include hard-to-specify animal behaviour[f]. May not be available for all statistical routines, e.g. conditional logistic regression except by weighting the log-likelihood for each location. 'Resamples' in environmental not geographical space
to inaccurate locations	generate random points within error polygon to estimate habitat mis-classification rate (i.e. bias matrix), invert and use to weight collected observations[a,o,k,n]	provides more reasonable estimate of uncertainty around habitat use estimates. Effects vary given degree of habitat fragmentation	improper error distribution can exacerbate noise or introduce bias; effects vary given degree of habitat fragmentation
complete trajectories by			
dead-reckoning	record speed, heading, and depth from known position (could be release site or GPS location) to project path in areas where physical location not observable[e]	accurate in marine systems where speed and depth recorded accurately[e]; might be used to infer animal path over short distances where GPS imprecision has largest effect	subject to bias from skewed device attachments (miscalibaration) and drift; accurately measuring effective move distance difficult in terrestrial systems, but promising[e]
Brownian bridges	estimate probability of occurrence in area between collected GPS points as a function of diffusive spread[v]	accounts for measurement error when estimating certainty of area used by animal	assumes random direction and constant rate of movement between known locations
iterative simulation	Model P_{fix} as $\sim f$(habitat, collar brand make, time, season, animal behaviour); use P_{fix} to iteratively replace missing locations within domain bounded by adjacent fixes to complete animal paths; replicate due to uncertainty in simulation process, combine results using multiple imputation techniques[p]	reduces type-II errors and coefficient bias[p]; adaptable to various analytical approaches, including conditional logistic models, animal movement and home range models; physically replaces location in geographical and environmental space, and at time of missing location	fix acquisition model requires independent field study, and effects of animal behaviour difficult to parameterize; processing can be laborious; can be extended to include solution for imprecise locations by also resampling with error polygons when completing paths
simultaneously model data and process			
occupancy approach	simultaneous estimation of selection and detection given selection using maximum likelihood approach[w]	does not require independent model for P_{fix}; efficient estimator of selection given probability of detection; provides individual-based model of detection and selection	accounts for missed fix effect, but does not address measurement error

(*Continued.*)

Table 2. (*Continued.*)

proposed solution	description	benefits	considerations
state-space models	simultaneous estimation of observation and process model using Bayesian approach[x,y]	relies on previous information of location bias and imprecision; efficient estimator of complex animal behaviour given noisy data; can model missing and imprecise data[z]	complex analytical machinery
data-cloning	maximum likelihood alternative to Bayesian state-space models that relies on data replication[aa,ab]	same as for state-space models	same as state-space models

[a]Nams (1989); [b]Dussault *et al.* (1999); [c]Rettie & McLoughlin (1999); [d]Rempel & Rodgers (1997); [e]Wilson *et al.* (2007); [f]Lewis *et al.* (2007); [g]Jerde & Visscher (2005); [h]DeCesare *et al.* (2005); [i]Swain *et al.* (2008); [j]Cain *et al.* (2005); [k]Kenow *et al.* (2001); [l]McKenzie *et al.* (2009); [m]Visscher (2006); [n]Moen *et al.* (1996); [o]Samuel & Kenow (1992); [p]Frair *et al.* (2004); [q]Hebblewhite *et al.* (2007); [r]D'Eon *et al.* (2002); [s]D'Eon (2003); [t]Johnson *et al.* (1998); [u]Horne *et al.* (2007*b*); [v]Horne *et al.* (2007*a*); [w]Nielson *et al.* (2009); [x]Morales *et al.* (2004); [y]Jonsen *et al.* (2005); [z]Patterson *et al.* (2008); [aa]Lele *et al.* (2007); [ab]Ponciano *et al.* (2009).

Models of P_{fix} can be developed from stationary device tests (e.g. Frair *et al.* 2004; Hebblewhite *et al.* 2007), or from analysis of areas of successful and unsuccessful fixes during monitoring of free-ranging animals (e.g. Graves & Waller 2006). The former approach can be time-consuming, and requires replication across a range of environmental conditions. Even among devices of the same brand and manufacturing cycle, moderate variation in canopy and terrain conditions can affect the magnitude of missed fixes (e.g. Frair *et al.* 2004; Hebblewhite *et al.* 2007). Thus, P_{fix} models should be developed specific to the study area, time period, device make/model and fix schedule that characterize data collection from free-ranging animals. If data-screening based on PDOP is employed, censoring should be done prior to estimating the P_{fix} model so as to account for the full extent of habitat-biased data loss. The Graves & Waller (2006) approach has the potential advantage of implicitly accounting for animal behaviour when estimating P_{fix}, although the precise coordinates of a failed location attempt may often be unknown and, consequently, only coarse habitat effects might be evaluated. Moreover, the specific behaviour will also probably be unknown, therefore this approach could not illuminate the relative effects of behaviour versus local habitat on GPS functioning. Nevertheless, individual-based models of P_{fix} may implicitly rather than explicitly account for the interactive effects of animal behaviour and local habitat variation on GPS performance. Formal testing is required to evaluate how such a P_{fix} model performs when used for statistical corrections in selection models. An alternative to the stand-alone P_{fix} model was recently proposed by Nielson *et al.* (2009), where only GPS data collected from a free-ranging animal were used to independently estimate models for: (i) resource selection, and (ii) animal detection given selection in a manner similar to patch-occupancy models (table 2). The Nielson *et al.* (2009) method also requires a larger landscape grain, but successfully corrected selection coefficients given up to 50 per cent biased data loss. This approach is adaptable to conditional sampling designs and movement models that may not allow for location specific weights. More complicated model structures, such as hierarchical models, are not yet readily available, but population-level inference might instead be obtained using a two-stage approach as detailed in Fieberg *et al.* (2010).

To our knowledge there has been no comprehensive approach proposed to correct for both imprecise and biased missing locations in resource selection models. Iterative simulation seemingly provides the most flexible solution as it can be applied to sampling designs that do not allow location-specific weights, is adaptable to movement modelling approaches, and, importantly, replacing missing locations (Frair *et al.* 2004) and resampling imprecise locations (Samuel & Kenow 1992) might readily be accomplished simultaneously to complete realizations of animal paths that account for both types of error. Additional research is required to determine whether such an approach might sufficiently account for the interactive effects of animal behaviour and local habitat interactions in resource selection studies, or whether additional detail specific to animal behaviour needs to be included in P_{fix} models.

(b) *Animal movements*

Fundamental to models of animal movements are statistical distributions of move distance and direction (Turchin 1998). Using GPS-based locations, the distance moved, or step length (SL), requires two consecutive fixes, whereas the direction moved, or turn angle (TA), requires three consecutive fixes. If we assume the probability of a single fix, P, to be independent and identically distributed (ignoring issues of fix-rate bias), then the probability of recording a SL and TA is P^2 and P^3, respectively (Jerde & Visscher 2005), indicating that movement data may remain scarce even given relatively high fix rates. Moreover, SL and TA distributions are inherently noisy, a problem exacerbated by location imprecision. From a study design perspective, it is critical to consider measurement error in animal locations within the

context of the magnitude of animal movement (Jerde & Visscher 2005). For a more general, rather than species-specific perspective, it is useful to speak in terms of error standard deviations (s.d.) rather than absolute distance errors (both scaled in the same units). For example, given $\mathrm{var}(\sqrt{\{[(x,y)-(\bar{x},\bar{y})]^2\}}) = 100$, then the s.d. = 10 m and 5 error s.d.'s = 50 m absolute error. Using simulations, Jerde & Visscher (2005) showed that the observed SL is positively biased given very short moves (actual SL < 0.5 error s.d.), and given SL < 5 error s.d. it is difficult to conclude whether the animal has moved at all. Thus, assuming a location precision of ± 25 m, consecutive GPS fixes must be more than 125 m apart to reliably infer that the animal had moved. In their simulation, the effect of location imprecision became negligible given very large moves (SL > 100 error s.d.; Jerde & Visscher 2005; see also Ganskopp & Johnson 2007). Nevertheless, when combining sequences of SL's into longer movement paths, GPS-induced 'jitter' may increase the apparent tortuosity of animal paths (DeCesare *et al.* 2005), leading to an overestimate of the cumulative distance travelled (Kauhala & Tiilikainen 2002; DeCesare *et al.* 2005; Jerde & Visscher 2005; Ganskopp & Johnson 2007), and eroding the biological signal in the animal trajectory (Bradshaw *et al.* 2007).

Location imprecision has a relatively greater effect on estimates of TA versus SL, potentially causing analysts to conclude a directional bias in animal movement when actual SLs are short. In two different simulation studies (Jerde & Visscher 2005; Hurford 2009), analysts observed that TA estimates were routinely off by more than 160° when either SL making up the trio of consecutive fixes was short (SL < 0.5 error s.d.). However, with two consecutive SLs that were moderately long (SL > 5 error s.d.), TA estimates were routinely within 60° (Jerde & Visscher 2005), and on average the mean of the TA distribution approached the true mean (Hurford 2009). The effect of location imprecision on TA estimates also varies with the magnitude of the turn itself. For example, for wolves (*Canis lupus*), estimating an accurate TA required a minimum SL ≥ 1.03 error s.d. when the true TA was 90° but a SL ≥ 1.66 error s.d. when the true TA was 180° (Hurford 2009).

Resting bouts recorded by GPS devices are another potential source of large errors in movement analyses because a SL and TA will be estimated even when an animal remains stationary during the sampling interval (e.g. Ganskopp & Johnson 2007). Resting bouts have been identified using activity sensors combined with GPS (Pépin *et al.* 2004; Ungar *et al.* 2005; Schwager *et al.* 2007), minimum distance or acceleration thresholds (Frair *et al.* 2005; Ganskopp & Johnson 2007), or combinations of activity sensors, movements and other variables (Ungar *et al.* 2005; Ganskopp & Johnson 2007; Van Moorter *et al.* 2010). Once identified, resting bouts might be excluded, or treated differently, for analyses of animal movements. But we note that resting bouts and fine-scale foraging activities are often confounded when based on GPS-derived data (Pépin *et al.* 2004; Ungar *et al.* 2005).

Researchers generally recommend strategically setting fix intervals *a priori* (at the study-design phase) or temporally resampling collar data so as to ensure sufficient movement relative to location imprecision during each sampling interval (Jerde & Visscher 2005; Bradshaw *et al.* 2007; Ganskopp & Johnson 2007; table 2). For example, Jerde & Visscher (2005) considered elk having an average rate of movement of 2.5 m min^{-1} (approx. 150 m h^{-1}) and a GPS location imprecision of ± 20 m (at 1 s.d.; D'Eon *et al.* 2002), and concluded that elk locations more than 100–120 m apart would be required to yield accurate movement information. As such, collecting locations on a sub-hourly interval would not yield informative data on elk movements, whereas a 1 h or more interval might prove optimal. Obviously, very infrequent fix intervals may grossly underestimate total movement (Mills *et al.* 2006), or miss short-duration but long-distance forays. Thus, previous knowledge on species movement behaviour and the precision of GPS locations is the key to proper study design. Should fine-scale movements (below the resolution of GPS precision) be of particular interest, one might employ differential correction to improve location precision to within a few meters (e.g. Ganskopp & Johnson 2007), or seek alternative approaches to mapping animal movements between GPS fixes, such as using a Brownian Bridge (Horne *et al.* 2007*a*; see also Lonergan *et al.* 2009 for interpolation of Argos paths) or incorporating dead-reckoning technologies such as those commonly employed in marine applications (Wilson *et al.* 2007). Additional approaches to reduce the effects of location imprecision involve smoothing animal paths, either mechanistically such as by censoring out the 'jitter' caused by GPS imprecision, or phenomenologically such as by fitting a spline through the trajectory of locations (DeCesare *et al.* 2005; table 2). Using a straight-line test path and a hand-held GPS, DeCesare *et al.* (2005) identified that under high canopy conditions, a location at time $t+1$ that deviated less than 7.98 m from the straight line connecting the locations acquired at time t and $t+2$ was probably due to location error (given a 2 s sampling interval), and used this observation to censor locations. Although we have not yet seen these techniques applied to ecological questions for free-ranging animals, these approaches are akin to the process suggested by Turchin (1998) in which biological moves are extracted from recorded animal paths. The larger conceptual issue of discriminating between biological moves (animal choices) and empirical steps (simply connecting the dots) is beyond the scope of this review (but see Hebblewhite & Haydon 2010).

Too often the complexity of studying animal movements has led researchers to overlook the problems associated with data acquisition, especially the compounding effects of fix-rate bias and measurement error, and interactions between animal behaviour and the performance of GPS devices (see Brooks *et al.* 2008; Heard *et al.* 2008). One especially promising area of enquiry includes state-space models (table 2), which couples a probabilistic model of the sampling process (the observation model) with a mechanistic

model for animal movement (the process model; Patterson *et al.* 2008). In this approach an animal's future 'state', be that a spatial location or a behavioural mode (e.g. resting, foraging, migrating), is predicted as a function of its current state (using a Markovian process) weighted by the likelihood of observing the data (e.g. Forester *et al.* 2007, who modelled the effects of autocorrelation on the observation process). Although state-space models can accommodate the effects of both biased missing data and measurement error in the locations acquired (Patterson *et al.* 2008), we know of no empirical examples doing so for the study of animal movements using GPS-based locations (but see Jonsen *et al.* (2005) for an approach focused on Argos sampling errors; and Clark & Bjørnsad (2004) for a population time-series analogue). The analytical complexity of state-space models remains non-trivial, and although the conceptual and technical machinery may exist, these approaches are not readily accessible to most applied ecologists.

(c) *Home ranges*

The large number of fixes required to capture seasonal patterns of space use by animals (Girard *et al.* 2006), and the even more frequent fixes required to capture brief but long-distance forays (Mills *et al.* 2006; Kochanny *et al.* 2009), can be difficult to acquire using traditional radiotelemetry techniques. Thus, GPS devices provide an unprecedented ability to quantify animal home-range patterns (see Kie *et al.* 2010). Although location imprecision can influence estimates of home-range size and shape, as well as the relative location of peaks and valleys of the utility distribution (Kauhala & Tiilikainen 2002; Moser & Garton 2007; Börger *et al.* 2008), estimates of animal home ranges nevertheless appear largely robust to contemporary levels of GPS measurement error. Moser & Garton (2007) used a volume of intersection (VI) statistic (0 indicating no overlap and 1 indicating identical distributions) to compare home-range estimates using accurate and 'jittered' locations achieved via simulation. As expected, VI values increased with increasing sample sizes and decreased with the magnitude of location imprecision, with the effects on fixed kernel home-range estimates mediated to some degree by home-range size. Using an error ratio (ER) = median location precision ($CEP_{0.5}$)/home-range area (A), where $CEP_{0.5}$ and A are expressed in similar units (e.g. km and km^2), Moser & Garton (2007) demonstrated that the impact of location imprecision on home-range estimates was negligible given an $ER < 0.1$. This means that for an animal whose home-range averages 100 km^2, GPS locations having a median precision ≤ 940 m will yield accurate home-range estimates (likewise an average home size of 10 km^2 requires a median GPS precision of 94 m or less for accurate estimates). Thus, the home ranges of animals large enough to carry GPS devices are expected to be generally unaffected by contemporary levels of measurement error in the recorded locations. For comparative studies, Börger *et al.* (2006) suggested using an average measure of location precision within individual home ranges as a covariate to control for individual- and spatially varying GPS positional error.

Biased missing data, on the other hand, has the potential to severely bias estimates of home-range size and utility distributions (Horne *et al.* 2007*b*), depending upon the magnitude of fix-rate bias and its spatial variability. Horne *et al.* (2007*b*) suggested that spatially uniform fix rates, even if they are low, would not influence home-range estimates, but that estimates could become inaccurate when the probability of acquiring a fix either covers a broad range of values (e.g. 0.5–1.0), or when low observation rates are aggregated within one part of the home range. As such, smaller home ranges composed of relatively few homogeneous patches may be more influenced by fix-rate bias than larger, more heterogeneous home ranges. Horne *et al.* (2007*b*) detailed a sample weighting approach, where locations are weighted by $1/P_{fix}$ (similar to the approach for resource selection studies), which provided robust home-range estimates (see also Fieberg 2007; table 2). Applying the approach to telemetry data, Horne *et al.* (2007*b*) observed greater discrepancies between corrected and uncorrected home-range estimates for mule deer (*O. hemionus*) than black bear, with the latter species occupying larger and more heterogeneous home ranges.

The impact of fix-rate bias also varied among home-range estimators, with differences between corrected (by sample weighting) and uncorrected estimates (the 'true' home-range being unknown) of −0.25 per cent to +10 per cent for a bivariate normal model, −14.2 per cent to +19.2 per cent for a 2-mode bivariate normal mixture model, and −18.4 per cent to +16.8 per cent for a fixed-kernel home-range model (Horne *et al.* 2007*b*). One problem with P_{fix} models is their failure to account for particularly low collar returns under some environmental conditions (e.g. D'Eon 2003; Frair *et al.* 2004), and thus weighting alone may be insufficient to overcome large data losses in geographical space. The iterative simulation approach detailed by Frair *et al.* (2004) might thus provide a more robust alternative for home-range estimators.

4. CONCLUSIONS AND FUTURE DIRECTIONS

Animal location data acquired by GPS devices are indeed plentiful, and becoming increasingly precise, but nevertheless pose challenges for analyses of resource selection and space use by animals. In terrestrial deployments we can be certain that closed canopies and steep terrain interfere with satellite signals, inducing habitat-biased errors that include both missing and spatially imprecise animal locations. These errors can muddy inferences of habitat and space use by animals, but can also be overcome to varying degree *a priori* via proper study design (e.g. considering GPS imprecision in light of animal movement behaviour and the resolution of environmental data), or, alternatively, by employing any number of ad hoc statistical corrections. Researchers consistently neglect to explicitly consider GPS errors during the study-design phase, and typically conduct no corrections (justifying this because of high fix rates), or correct for one or the other type of error without

recognizing that errors propagate. That is, we collectively overlook the additive or compounding effects of location imprecision, fix-rate bias and, in the case of resource selection, the perhaps even more egregious problem of map inaccuracy on statistical inferences. It was our intention with this review to provide clarity on these issues so as to improve study designs and, by extension, the veracity of ecological insights gained from GPS-based location data. Nevertheless, more work is needed to understand how animal behaviour affects GPS functionality, along with more rigorous testing of solutions that address the combined effects of location imprecision and fix-rate bias in ecological analyses. In light of these issues, two analytical approaches seem particularly appealing: (i) iterative simulation to complete animal paths, combined with spatial resampling of locations prior to analysing patterns in the data, and (ii) state-space models that simultaneously model the observation process as well as the ecological process of interest. In contrast to sample weighting, these approaches show promise for resolving GPS problems in geographical as well as environmental space, implicitly including animal behaviour in the analytical solution. Yet, these approaches remain underused due in large part to their non-trivial levels of complexity. We commend authors who provide scripts, code and workshops to make these approaches more accessible to ecologists. It remains unclear, however, whether ever-increasing analytical complexity is really necessary to account for GPS errors in ecological analyses. Perhaps censoring gross positional errors based on PDOP values and weighting hard-to-acquire locations provides an equally satisfying solution. As technologies continue to improve, GPS errors will diminish. But rather than assume GPS location data to be hunky-dory and without error, or to immediately invest in potentially expensive and complicated solutions, we suggest that analysts might benefit most by testing the sensitivity of their models to the probable causes and magnitudes of GPS errors specific to their collar brand, study area, species and ecological question.

We recognize the Edmund Mach Foundation for hosting the 2008 GPS Workshop in Trento, Italy, that led to this series of papers, as well as discussions among the workshop attendees that strengthened this review. Comments from anonymous reviewers also greatly improved this manuscript. SUNY ESF provided partial travel support for the lead author.

REFERENCES

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. 2008 Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* **31**, 140–160. (doi:10.1111/j.2007.0906-7590.05236.x)

Anderson, C. R. & Lindzey, F. G. 2003 Estimating cougar predation rates from GPS location clusters. *J. Wildlife Manage.* **67**, 307–316. (doi:10.2307/3802772)

Beyer, D. E. & Haufler, J. B. 1994 Diurnal versus 24-hour sampling of habitat use. *J. Wildlife Manage.* **58**, 178–180. (doi:10.2307/3809566)

Biggs, J. R., Bennett, K. D. & Fresquez, P. R. 2001 Relationship between home range characteristics and the probability of obtaining successful global positioning system (GPS) collar positions for elk in New Mexico. *West. N. Am. Nat.* **61**, 213–222.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. 2006 Effects of sampling regime on the mean and variance of home range size estimates. *J. Anim. Ecol.* **75**, 1393–1405. (doi:10.1111/j.1365-2656.2006.01164.x)

Börger, L., Dalziel, B. D. & Fryxell, J. M. 2008 Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.* **11**, 637–650. (doi:10.1111/j.1461-0248.2008.01182.x)

Bowman, J. L., Kochanny, C. O., Demarais, S. & Leopold, B. D. 2000 Evaluation of a GPS collar for white-tailed deer. *Wildlife Soc. B* **28**, 141–145.

Boyce, M. S., Turner, M. G., Fryxell, J. & Turchin, P. 2003 Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* **10**, 421–431.

Bradshaw, C. J. A., Sims, D. W. & Hays, G. C. 2007 Measurement error causes scale-dependent threshold erosion of biological signals in animal movement data. *Ecol. Appl.* **17**, 628–638. (doi:10.1890/06-0964)

Brooks, C., Bonyongo, C. & Harris, S. 2008 Effects of global positioning system collar weight on zebra behavior and location error. *J. Wildlife Manage.* **72**, 527–534.

Cagnacci, F., Boitani, L., Powell, R. A. & Boyce, M. S. 2010 Animal ecology meets GPS-based radiotelemetry: a perfect storm of oppurtunities and challenges. *Phil. Trans. R. Soc. B* **365**, 2157–2162. (doi:10.1098/rstb.2010.0107).

Cain, J. W., Krausman, P. R., Jansen, B. D. & Morgart, J. R. 2005 Influence of topography and GPS fix interval on GPS collar performance. *Wildlife Soc. B* **33**, 926–934. (doi:10.2193/0091-7648(2005)33[926:IOTAGF]2.0.CO;2)

Cargnelutti, B., Coulon, A., Hewison, A. J. M., Goulard, M., Angibault, J. M. & Morellet, N. 2007 Testing Global Positioning System performance for wildlife monitoring using mobile collars and known reference points. *J. Wildlife Manage.* **71**, 1380–1387.

Clark, J. S. & Bjørnsad, O. N. 2004 Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology* **85**, 3140–3150. (doi:10.1890/03-0520)

Conner, L. M., Smith, M. D. & Burger, L. W. 2003 A comparison of distance-based and classification-based analyses of habitat use. *Ecology* **84**, 526–531. (doi:10.1890/0012-9658(2003)084[0526:ACODBA]2.0.CO;2)

Conner, L. M., Smith, M. D. & Burger, L. W. 2005 A comparison of distance-based and classification-based analyses of habitat use: reply. *Ecology* **86**, 3125–3129. (doi:10.1890/05-0760)

DeCesare, N. J., Squires, J. R. & Kolbe, J. A. 2005 Effect of forest canopy on GPS-based movement data. *Wildlife Soc. B* **33**, 935–941. (doi:10.2193/0091-7648(2005)33[935:EOFCOG]2.0.CO;2)

D'Eon, R. G. 2003 Effects of a stationary GPS fix-rate bias on habitat selection analyses. *J. Wildlife Manage.* **67**, 858–863. (doi:10.2307/3802693)

D'Eon, R. G. & Delparte, D. 2005 Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *J. Appl. Ecol.* **42**, 383–388. (doi:10.1111/j.1365-2664.2005.01010.x)

D'Eon, R. G. & Serrouya, R. 2005 Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. *J. Mammal.* **86**, 736–744. (doi:10.1644/1545-1542(2005)086[0736:MDSMAM]2.0.CO;2)

D'Eon, R. G., Serrouya, R., Smith, G. & Kochanny, C. O. 2002 GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Soc. B* **30**, 430–439.

Dussault, C., Courtois, R., Ouellet, J. P. & Huot, J. 1999 Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. *Wildlife Soc. B* **27**, 965–972.

Dussault, C., Courtois, R., Huot, J. & Ouellet, J. P. 2001 The use of forest maps for the description of wildlife habitats: limits and recommendations. *Can. J. Forest Res.* **31**, 1227–1234. (doi:10.1139/cjfr-31-7-1227)

Dussault, C., Ouellet, J. P. & Courtois, R. 2005 A comparison of distance-based and classification-based analyses of habitat use: comment. *Ecology* **86**, 3119–3125. (doi:10.1890/05-0203)

Edenius, L. 1997 Field test of a GPS location system for moose (*Alces alces*) under Scandinavian boreal conditions. *Wildlife Biol.* **3**, 39–43.

Fieberg, J. 2007 Utilization distribution estimation using weighted kernel density estimators. *J. Wildlife Manage.* **71**, 1669–1675.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M. S. & Frair, J. L. 2010 Correlation and studies of habitat selection: problem, red herring, or opportunity? *Phil. Trans. R. Soc. B* **365**, 2233–2244. (doi:10.1098/rstb.2010.0079)

Findholt, S. L., Johnson, B. K., McDonald, L. L., Kern, J. W., Ager, A., Stussy, R. J. & Bryant, L. D. 2002 Adjusting for radiotelemetry error to improve estimates of habitat use. *USDA Forest Service Pacific Northwest Research Station Research Paper.*

Forester, J. D., Ives, A. R., Turner, M. G., Anderson, D. P., Fortin, D., Beyer, H. L., Smith, D. W. & Boyce, M. S. 2007 State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecol. Monogr.* **77**, 285–299. (doi:10.1890/06-0534)

Frair, J. L., Nielsen, S. E., Merrill, E. H., Lele, S. R., Boyce, M. S., Munro, R. H. M., Stenhouse, G. B. & Beyer, H. L. 2004 Removing GPS collar bias in habitat selection studies. *J. Appl. Ecol.* **41**, 201–212. (doi:10.1111/j.0021-8901.2004.00902.x)

Frair, J. L., Merrill, E. H., Visscher, D. R., Fortin, D., Beyer, H. L. & Morales, J. M. 2005 Scales of movement by elk (Cervus elaphus) in response to heterogeneity in forage resources and predation risk. *Landscape Ecol.* **20**, 273–287. (doi:10.1007/s10980-005-2075-8)

Fryxell, J. M., Hazell, M., Borger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T. & Rosatte, R. C. 2008 Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proc. Natl Acad. Sci. USA* **105**, 19 114–19 119. (doi:10.1073/pnas.0801737105)

Gau, R. J. *et al.* 2004 Uncontrolled field performance of Televilt GPS-Simplex (TM) collars on grizzly bears in western and northern Canada. *Wildlife Soc. B* **32**, 693–701. (doi:10.2193/0091-7648(2004)032[0693:UFPOTG]2.0.CO;2)

Ganskopp, D. C. & Johnson, D. D. 2007 GPS error in studies addressing animal movements and activities. *Rangeland Ecol. Manage.* **60**, 350–358. (doi:10.2111/1551-5028(2007)60[350:GEISAA]2.0.CO;2)

Girard, I., Dussault, C., Ouellet, J. P., Courtois, R. & Caron, A. 2006 Balancing number of locations with number of individuals in telemetry studies. *J. Wildlife Manage.* **70**, 1249–1256.

Graves, T. A. & Waller, J. S. 2006 Understanding the causes of missed global positioning system telemetry fixes. *J. Wildlife Manage.* **70**, 844–851.

Hansen, M. C. & Riggs, R. A. 2008 Accuracy, precision, and observation rates of global positioning system telemetry collars. *J. Wildlife Manage.* **72**, 518–526.

Heard, D. C., Ciarniello, L. M. & Seip, D. R. 2008 Grizzly bear behavior and global positioning system collar fix rates. *J. Wildlife Manage.* **72**, 596–602.

Hebblewhite, M. & Haydon, D. T. 2010 Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Phil. Trans. R. Soc. B* **365**, 2303–2312. (doi:10.1098/rstb.2010.0087)

Hebblewhite, M. & Merrill, E. H. 2007 Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* **152**, 377–387. (doi:10.1007/s00442-007-0661-y)

Hebblewhite, M., Percy, M. & Merrill, E. H. 2007 Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the Central Canadian Rockies. *J. Wildlife Manage.* **71**, 2026–2033.

Horne, J. S., Garton, E. O., Krone, S. M. & Lewis, J. S. 2007*a* Analyzing animal movements using Brownian bridges. *Ecology* **88**, 2354–2363. (doi:10.1890/06-0957.1)

Horne, J. S., Garton, E. O. & Sager-Fradkin, K. A. 2007*b* Correcting home-range models for observation bias. *J. Wildlife Manage.* **71**, 996–1001.

Hurford, A. 2009 GPS measurement error gives rise to spurious 180° turning angles and strong directional biases in animal movement data. *PLoS ONE* **4**, e5632. (doi:10.1371/journal.pone.0005632)

Jerde, C. L. & Visscher, D. R. 2005 GPS measurement error influences on movement model parameterization. *Ecol. Appl.* **15**, 806–810. (doi:10.1890/04-0895)

Jiang, Z., Sugita, M., Kitahara, M., Takatsuki, S., Goto, T. & Yoshida, Y. 2008 Effects of habitat feature, antenna position, movement, and fix interval on GPS radio collar performance in Mount Fuji, central Japan. *Ecol. Res.* **23**, 581–588. (doi:10.1007/s11284-007-0412-x)

Johnson, B. K., Ager, A. A., Findholt, S. L., Wisdom, M. J., Marx, D. B., Kern, J. W. & Bryant, L. D. 1998 Mitigating spatial differences in observation rate of automated telemetry systems. *J. Wildlife Manage.* **62**, 958–967. (doi:10.2307/3802548)

Johnson, C. J., Heard, D. C. & Parker, K. L. 2002*a* Expectations and realities of GPS animal location collars: results of three years in the field. *Wildlife Biol.* **8**, 153–159.

Johnson, C. J., Parker, K. L., Heard, D. C. & Gillingham, M. P. 2002*b* A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecol. Appl.* **12**, 1840–1860. (doi:10.1890/1051-0761(2002)012[1840:AMBATU]2.0.CO;2)

Johnson, C. J. & Gillingham, M. P. 2008 Sensitivity of species-distribution models to error, bias, and model design: an application to resource selection functions for woodland caribou. *Ecol. Model.* **213**, 143–155. (doi:10.1016/j.ecolmodel.2007.11.013)

Jonsen, I. D., Flemming, J. M. & Myers, R. A. 2005 Robust state-space modeling of animal movement data. *Ecology* **86**, 2874–2880. (doi:10.1890/04-1852)

Kauhala, K. & Tiilikainen, T. 2002 Radio location error and the estimates of home-range size, movements, and habitat use: a simple field test. *Ann. Zool. Fenn.* **39**, 317–324.

Keating, K. A., Brewster, W. G. & Key, C. H. 1991 Satellite telemetry: performance of animal-tracking systems. *J. Wildlife Manage.* **55**, 160–171. (doi:10.2307/3809254)

Kenow, K. P., Wright, R. G., Samuel, M. D. & Rasmussen, P. W. 2001 Integrating SAS and GIS software to improve habitat-use estimates from radiotelemetry data. *Wildlife Soc. B* **29**, 1006–1009.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J.-M. & Moorcroft, P. R. 2010 The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Phil. Trans. R. Soc. B* **365**, 2221–2231. (doi:10.1098/rstb.2010.0093)

Kochanny, C. O., Delguidice, G. D. & Fieberg, J. 2009 Comparing global positioning system and very high

frequency telemetry home ranges of white-tailed deer. *J. Wildlife Manage.* **73**, 779–787.

Kufeld, R. C., Bowden, D. C. & Siperek, J. M. 1987 Evaluation of a telemetry system for measuring habitat usage in mountainous terrain. *Northwest Sci.* **61**, 249–256.

Lele, S. R., Dennis, B. & Lutscher, F. 2007 Data cloning: easy maximum likelihood estimation for complex ecological models using Bayesian Markov Chain Monte Carlo methods. *Ecol. Lett.* **10**, 551–563. (doi:10.1111/j.1461-0248.2007.01047.x)

Lewis, J. S., Rachlow, J. L., Garton, E. O. & Vierling, L. A. 2007 Effects of habitat on GPS collar performance: using data screening to reduce location error. *J. Appl. Ecol.* **44**, 663–671. (doi:10.1111/j.1365-2664.2007.01286.x)

Lindberg, M. S. & Walker, J. 2007 Satellite telemetry in avian research and management: sample size considerations. *J. Wildlife Manage.* **71**, 1002–1009.

Lonergan, M., Fedak, M. & McConnell, B. 2009 The effects of interpolation error and location quality on animal track reconstruction. *Mar. Mammal Sci.* **25**, 275–282. (doi:10.1111/j.1748-7692.2008.00264.x)

Marzluff, J. M., Vekasy, M. S. & Coody, C. 1994 Comparative accuracy of aerial and ground telemetry locations of foraging raptors. *Condor* **96**, 447–454. (doi:10.2307/1369327)

Mayaux, P. *et al.* 2006 Validation of the global land cover 2000 map. *IEEE Trans. GeoSci. Remote* **44**, 1728–1739. (doi:10.1109/TGRS.2006.864370)

McKenzie, H. W., Jerde, C. L., Visscher, D. R., Merrill, E. H. & Lewis, M. A. 2009 Inferring linear feature use in the presence of GPS measurement error. *Environ. Ecol. Stat.* **16**, 531–546. (doi:10.1007/s10651-008-0095-7)

Merrill, E., Sand, H., Zimmermann, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P. & Frair, J. L. 2010 Building a mechanistic understanding of predation with GPS-based movement data. *Phil. Trans. R. Soc. B* **365**, 2279–2288. (doi:10.1098/rstb.2010.0077)

Mills, K. J., Patterson, B. R. & Murray, D. L. 2006 Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. *Wildlife Soc. B* **34**, 1463–1469. (doi:10.2193/0091-7648(2006)34[1463:EOVSFO]2.0.CO;2)

Moen, R., Pastor, J., Cohen, Y. & Schwartz, C. C. 1996 Effects of moose movement and habitat use on GPS collar performance. *J. Wildlife Manage.* **60**, 659–668. (doi:10.2307/3802085)

Morales, J. M., Haydon, D. T., Frair, J., Holsiner, K. E. & Fryxell, J. M. 2004 Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**, 2436–2445. (doi:10.1890/03-0269)

Moser, B. W. & Garton, E. O. 2007 Effects of telemetry location error on space-use estimates using a fixed-kernel density estimator. *J. Wildlife Manage.* **71**, 2421–2426.

Nams, V. O. 1989 Effects of radiotelemetry error on sample size and bias when testing for habitat selection. *Can. J. Zool.* **67**, 1631–1636. (doi:10.1139/z89-233)

Nielson, R. M., Manly, B. F. J., McDonald, L. L., Sawyer, H. & McDonald, T. L. 2009 Estimating habitat selection when GPS fix success is less than 100%. *Ecology* **90**, 2956–2962. (doi:10.1890/08-1562.1)

North, M. P. & Reynolds, J. H. 1996 Microhabitat analysis using radiotelemetry locations and polytomous logistic regression. *J. Wildlife Manage.* **60**, 639–653. (doi:10.2307/3802083)

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. 2008 State-space models of individual animal movement. *Trends Ecol. Evol.* **23**, 87–94. (doi:10.1016/j.tree.2007.10.009)

Pépin, D., Adrados, C., Mann, C. & Janeau, G. 2004 Assessing real daily distance traveled by ungulates using differential GPS locations. *J. Mammal.* **85**, 774–780. (doi:10.1644/BER-022)

Ponciano, J. M., Taper, M. L., Dennis, B. & Lele, S. R. 2009 Hierarchical models in ecology: confidence intervals, hypothesis testing, and model selection using data cloning. *Ecology* **90**, 356–362. (doi:10.1890/08-0967.1)

Rempel, R. S. & Rodgers, A. R. 1997 Effects of differential correction on accuracy of a GPS animal location system. *J. Wildlife Manage.* **61**, 525–530. (doi:10.2307/3802611)

Rempel, R. S., Rodgers, A. R. & Abraham, K. F. 1995 Performance of a GPS animal location system under boreal forest canopy. *J. Wildlife Manage.* **59**, 543–551. (doi:10.2307/3802461)

Rettie, W. J. & McLoughlin, P. D. 1999 Overcoming radiotelemetry bias in habitat-selection studies. *Can. J. Zool.* **77**, 1175–1184. (doi:10.1139/cjz-77-8-1175)

Rodgers, A. R., Rempel, R. S. & Abraham, K. F. 1996 A GPS-based telemetry system. *Wildlife Soc. B.* **24**, 559–566.

Rumble, M. A. & Lindzey, F. 1997 Effects of forest vegetation and topography on global positioning system collars for elk. *Resource Technol. Inst. Symp.* **4**, 492–501.

Sager-Fradkin, K. A., Jenkins, K. J., Hoffman, R. A., Happe, P. J., Beecham, J. J. & Wright, R. G. 2007 Fix success and accuracy of global positioning system collars in old-growth temperate coniferous forests. *J. Wildlife Manage.* **71**, 1298–1308.

Samuel, M. D. & Kenow, K. P. 1992 Evaluating habitat selection with radiotelemery triangulation error. *J. Wildlife Manage.* **56**, 725–734. (doi:10.2307/3809466)

Schwager, M., Anderson, D. M., Butler, Z. & Rus, D. 2007 Robust classification of animal tracking data. *Comput. Electron. Agric.* **56**, 46–59. (doi:10.1016/j.compag.2007.01.002)

Stehman, S. V., Wickham, J. D., Smith, J. H. & Yang, L. 2003 Thematic accuracy of the 1992 national land--cover data for the eastern United States: statistical methodology and regional results. *Remote Sens. Environ.* **86**, 500–516. (doi:10.1016/S0034-4257(03)00128-7)

Swain, D. L., Wark, T. & Bishop-Hurley, G. J. 2008 Using high fix rate GPS data to determine the relationships between fix rate, prediction errors, and patch selection. *Ecol. Model.* **212**, 273–279. (doi:10.1016/j.ecolmodel.2007.10.027)

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. & Bates, K. K. 2010 Global positioning system and associated technologies in animal behaviour and ecological research. *Phil. Trans. R. Soc. B* **365**, 2163–2176. (doi:10.1098/rstb.2010.0090)

Turchin, P. 1998 *Quantitative analysis of movement: measuring and modling population redistribution in animals and plants*. Sunderland, MA: Sinauer Associates.

Ungar, E. D., Henkin, Z., Gutman, M., Dolev, A., Genizi, A. & Ganskopp, D. 2005 Inference of animal activity from GPS collar data on free-ranging cattle. *Rangeland Ecol. Manage.* **58**, 256–266. (doi:10.2111/1551-5028(2005)58[256:IOAAFG]2.0.CO;2)

Urbano, F., Cagnacci, F., Calenge, C., Dettki, H., Cameron, A. & Neteler, M. 2010 Wildlife tracking data management: a new vision. *Phil. Trans. R. Soc. B* **365**, 2177–2185. (doi:10.1098/rstb.2010.0081)

Van Moorter, B., Visscher, D. R., Jerde, C. L., Frair, J. L. & Merrill, E. H. 2010 Identifying movement states from location data using cluster analysis. *J. Wildlife Manage.* **74**, 588–594. (doi:10.2193/2009-155)

Villepique, J. T., Bleich, V. C., Pierce, B. M., Stephenson, T. R., Botta, R. A. & Bowyer, R. T. 2008 Evaluating GPS

collar error: a critical evaluation of Televilt POSREC-Science (TM) collars and a method for screening location data. *Calif. Fish Game* **94**, 155–168.

Visscher, D. R. 2006 GPS measurement error and resource selection functions in a fragmented landscape. *Ecography* **29**, 458–464.

White, G. C. & Garrott, R. A. 1986 Effects of biotelemetry triangulation error on detecting habitat selection. *J. Wildlife Manage.* **50**, 509–513. (doi:10.2307/3801114)

White, G. C. & Garrott, R. A. 1990 *Analysis of wildlife radio-tracking data*. San Diego, CA: Academic Press.

Wickham, J. D., Stehman, S. V., Smith, J. H. & Yang, L. 2004 Thematic accuracy of the 1992 national land-cover data for the western United States. *Remote Sens. Environ.* **91**, 452–468. (doi:10.1016/j.rse.2004.04.002)

Wilson, R. P. *et al.* 2007 All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Res. Pt. II* **54**, 193–210.

Zimmerman, J. W. & Powell, R. A. 1995 Radiotelmetry error: location error method compared with error polygons and confidence ellipses. *Can. J. Zool.* **73**, 1123–1133. (doi:10.1139/z95-134)